ZONATION PATTERNS IN THE POTHOLES OF KALSOW PRAIRIE, IOWA

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Abstract.— Kalsow Prairie, a mesic prairie remnant in central Iowa, was acquired by the state in 1949 and later established as a botanical reserve. This study concerns a complex of 14 potholes and adjacent drainage areas within the prairie. The potholes varied in depth and degree of fill and are thus useful in studies of plant succession. All 14 potholes exhibit zonation patterns. A total of 36 transects were taken in the various community zones. Canopy cover data were taken in every zone. The zones are ordinated into three-dimensional space as well as clustered. Interspecific association patterns are elucidated. A successional sequence is proposed.

There are prairies three, six, ten, and twenty leagues in length, and three in width, surrounded by forests of the same extent; beyond these, the prairies begin again, so that there is as much of one sort of land as of the other. Sometimes we saw the grass very short, and, at other times five or six feet high; hemp, which grows naturally there, reaches a height of eight feet.

A settler would not there spend ten years in cutting down and burning trees; on the day of his arrival, he could put his plough into the ground. (Louis Jolliet)

These are the finest and most fertile countries in the world. . . . From time to time there are vast prairies where the grass is ten or twelve feet high at all seasons. . . . No settler arriving in the country will not find at first enough to support plenteously a large family, or will not, in less than two years' time be as comfortably settled as in any place in Europe. (Douay)

Such are the early accounts from explorers and settlers of presettlement Iowan vegetation (Dondore 1926). A government survey begun in March 1832, when Iowa was still a territory, and completed in August 1859, first documented the original extent of this vast grassland area. That survey indicated that in the 1850s about 85 percent of Iowa was covered by grassland (U.S. Government 1868, Hayden 1945, Hewes 1950, Dick-Peddie 1955).

Accounts by the first explorers, surveyors, and settlers in the area describe three major types of landscape in Iowa: (1) woodland, (2) well-drained prairie, and (3) poorly drained prairie and marsh (Dondore 1926, Berry 1927, Hewes 1950). The woodlands were confined to stream valleys and adjacent slopes, and the prairie was said to occupy the remaining portions of the land (Berry 1927, Hewes 1950). The well-drained prairie areas were the most extensive except in portions of the state subjected to late Wisconsinan glaciation; there the poorly drained prairie and marsh were more common (Hewes 1950, Hewes 1951, Hewes and Frandson 1952). The well-drained prairie was described as highly fertile (Dondore 1926, Berry 1927), whereas the poorly drained prairie was filled with water most of the season and "capable of producing nothing but wild rice, frogs, and mosquitoes" (Hewes and Frandson 1952).

The characteristics of Iowa prairie in terms of vegetation types, structure, and general ecology of the dominant species were the subjects of several papers during the 1930s and 1940s (Steiger 1930, Rydberg 1931, Weaver and Fitzpatrick 1934, Hayden 1943). These authors recognized the existence of six grassland communities and generally con cluded that water relations, as affected by climate, soil, and topography, were responsible for local variations in the structure and distribution of prairie vegetation. "In varying the water relations of soil and air they merely bring about changes in the groupings of the dominant grasses and accompanying segregations and rearrangements of the forbs" (Weaver and Fitzpatrick, 1934).

The major grassland types as alluded to in the above studies were labeled "consociations" after Weaver and Clements (1938) and were designated as follows:

1. Big Bluestem type (*Andropogon gerardi*)—found on the lower moist slopes and well-aerated lowlands.
2. Slough Grass type (*Spartina pectinata*)—found on poorly aerated and wet soils of sloughs and natural drainage systems.

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3. Tall panic grass-wildrye type (*Panicum virgatum* and *Elymus canadensis*)—found on soils intermediate between Slough Grass and Big Bluestem types.
4. Little Bluestem type (*Schizocherium scoparius*)—most important upland type on well-drained soils.
5. Needle Grass type (*Stipa spartea*)—found on the uplands, often occurring as a narrow zone following the shoulders of ridges.
6. Prairie dropseed type (*Sporobolus heterolepis*)—found locally on the driest upland sites.

Moyer (1953), Aikman and Thorne (1956), Ehrenreich (1957), and Kennedy (1969) have presented ecological and taxonomic descriptions of four state-owned native prairie tracts. The vegetation complexes studied were basically limited to upland prairie. Those studies include information on soils, microclimate, topography, and management, as well as extensive literature reviews.

These prairies are presently owned by state agencies and were purchased and set aside as natural areas with the intent that the various typical landscapes, wild flowers, and wildlife of the native tall-grass prairie region be preserved for posterity. It was also intended that these areas serve as game and wildlife sanctuaries; as examples of the native prairie soil types, where comparisons could be made with cultivated soils of the same soil association; and as prairie reserves where scientific investigations could be undertaken on problems concerning the native flora and fauna of the various topographic, climatic, and prairie districts throughout Iowa. The prairies were also meant to serve as reference points by which future generations could compare the postsettlement influences of man on Iowa (Hayden 1946, Moyer 1953, Aikman 1959, Landers 1966).

One such area is Kalsow Prairie, 160 acres of unplowed grassland in Pocahontas County, Iowa. Criteria for its purchase dictated that this area satisfy the requirements of a game preserve, contain one or more soil types of an association, and include several regional vegetation types (Hayden 1946). The prairie was purchased in 1949 by the Iowa State Conservation Commission and since its purchase has been the object of several studies dealing with its vegetation, soils, management, insects, response to fire, mammals, and nematodes (Moyer 1953, Ehrenreich 1957, Esau 1968, Richards 1969, Brennan 1969, Norton and Ponchillia 1968, Schmitt 1969).

The present investigation was undertaken to provide information on the phytosociology and ecological relationships of poorly drained prairie and marsh areas of Kalsow Prairie. It includes information on species composition and distribution, zonation patterns, and interrelationships within and between these zones.

Methods

General

This study was begun in the spring of 1967 and continued through the following year (1968) and into the summer of 1969. Kalsow Prairie is one of four state-owned Iowa prairies. It is located five miles northwest of Manson, Iowa, and comprises the NE ¼ of Section 36, Belleville Township, T 90N, R 32W, Pocahontas County. It occurs in a part of north central Iowa that was glaciated during the most recent advances of the Wisconsinan glaciation and within the Clarion-Nicollet-Webster soil association area (Ruhe 1969). The area was chosen for study on the basis of its vegetational composition, i.e., floristic richness and the presence of several pothole areas (poorly drained prairie and marsh).

Taxonomy

Voucher specimens were collected in duplicate throughout the growing seasons of 1967 and 1968. All specimens were identified, and identical sets have been deposited in the herbaria of Iowa State University, Ames, Iowa, and Brigham Young University, Provo, Utah. Nomenclature follows Pohl (1966) for the grasses, Gilly (1946) for the sedges, and Gleason (1952) for the forbs.

Community Types

Kalsow Prairie contains within its boundaries a complex of potholes and corresponding drainage ways. The vegetation of these community types was analyzed using two separate approaches. The first involved the identification and listing of all species, and the second utilized random sample plots to determine percent cover, composition, and interspecific relationships of species within these subcommunities.

Quadrat Analysis

The vegetation of each area was sampled by using a 20 × 50 cm (1000 cm^2) quadrat. Twenty quadrats were located along transects on a restricted basis to reduce bias and

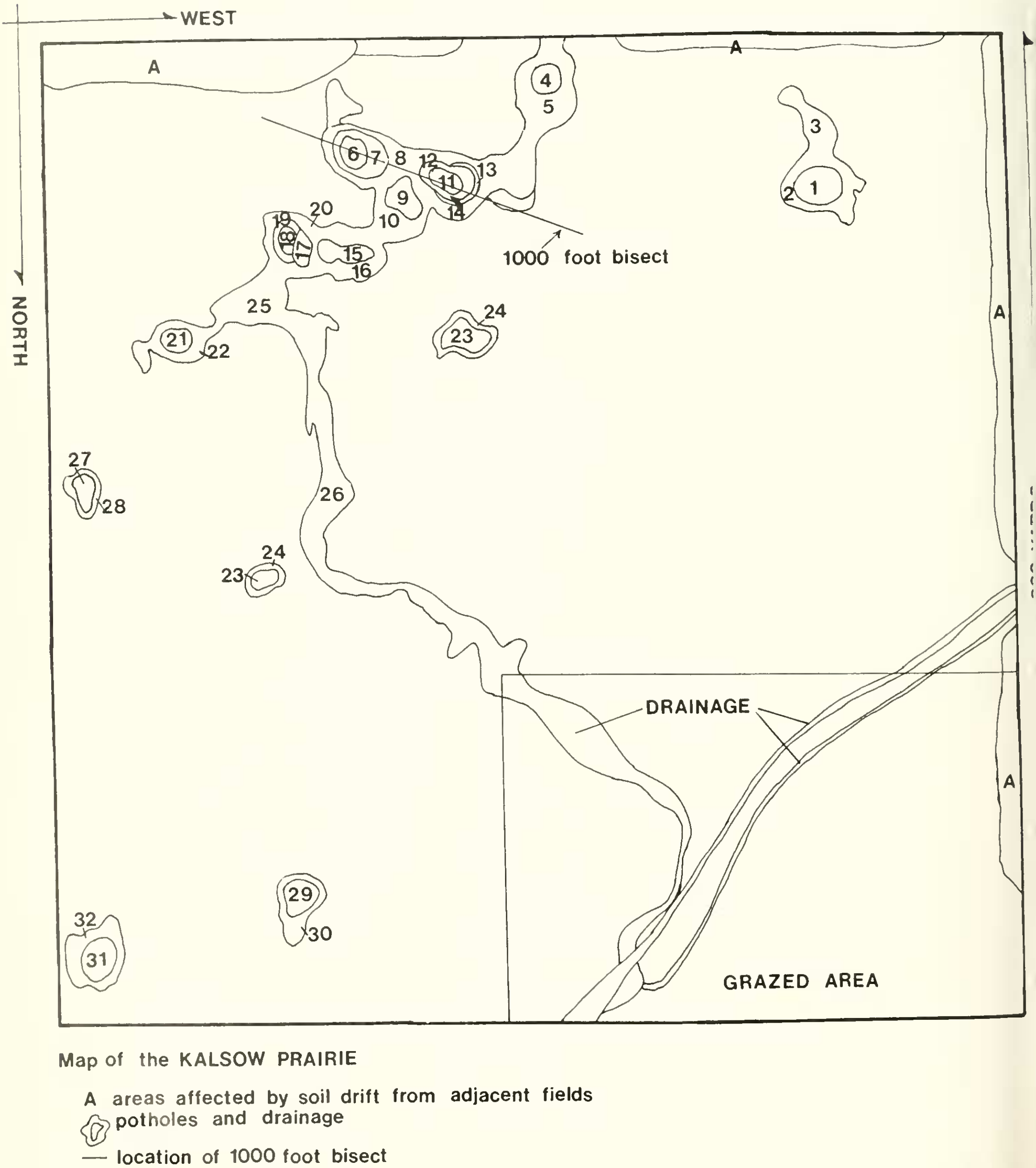

Fig. 1. Map of Kalsow Prairie showing locations of potholes and drainage ways.

to keep adjacent quadrats at fairly equal distances apart. The number of samples varied with the subcommunity or zone, but a total of 720 quadrats were taken within the community. Sampling was done between 1 August and 15 September each year when most species had reached their maximum growth. Cover estimates were made for each quadrat through use of Daubenmire's (1959) method.

Coverage was determined separately for all species overlapping the plot regardless of where the individuals were rooted. Coverage was projected to include the perimeter of overlap of each species regardless of superimposed canopies of other species. The canopies of different species were commonly interlaced or superimposed over the same area; therefore coverage percents often total greater than 100 percent.

Community Analysis

Analysis of these areas was accomplished by dividing the sites into subunits or zones (Fig. 1) based upon location and dominant species. Each subunit was then sampled by randomly locating a starting point and then placing a quadrat every 3 m along a transect. Twenty quadrats were taken for each zone.

Data Analysis

General descriptive data.— Data collected from quadrat, mapping, and topographic studies were used to describe the vegetation of each zone. Frequency values and average cover values were determined for all species in every stand. Cover values were determined by summing the midpoints of the cover-class ranges and dividing by the number of sample quadrats in each zone.

Ordination analysis.— An ordination technique proposed by Orloci (1966) was employed to ordinate vegetation units within the different subcommunities listed above. Raw data were first summarized by hand calculation and then transferred to punch cards. The entities to be ordinated (i.e., plant species or stands of vegetation) were projected as points into n-dimensional space. Such points were positioned by attribute scores through the application of the R and Q-techniques of factor analysis (Orloci 1967). Once established, this multidimensional array of points was then reduced to a three-dimensional system. This was accomplished by selecting the two most different stands or species and placing one at zero and the other at some distance along the abscissa. All other stands or species under consideration were then positioned linearly in relationship to these two extremes. This action thus established the X-axis. The above process was repeated until all points had been established in three-dimensional space (i.e., Y and Z axes had been added). Coordinate values for the X, Y, and Z axes were given as output from the computer.

Cluster analysis.— Cluster analyses were performed by calculating a similarity index (SI) (Ruzicka 1958) in percent from the formula:

$$SI = \frac{\Sigma \min (Xi, Yi)}{\Sigma \max (Xi, Yi)}$$

and then clustering the indices using unweighted pair-group clustering techniques (UPGMA) (Sneath and Sokal 1973). The UPGMA method computes the average similarity of each unit to the cluster, using arithmetic averages. It is widely used and has been found to introduce less distortion than other methods (Kaesler and Cairns 1972).

Interspecific association analysis.— Expressions of interspecific association were attempted using Cole's Index (1949). Step one in the computation of the index involved the accumulation of 2 × 2 contingency tables (Fig. 7). Actual calculation of the index involved the following three sets of formulas:

when ad $\leq$ bc:

$$C_7 \pm Sdc = \frac{ad-bc}{(a+b)(b+d)} \pm \frac{(a+c)(c+d)}{n(a+b)(b+c)}$$

when bc $>$ ad and d $\leq$ a:

$$C_7 \pm Sdc = \frac{ad-bc}{(a+b)(a+c)} \pm \frac{(b+d)(c+d)}{n(a+b)(a+c)}$$

when bc $>$ ad and a $>$ d:

$$C_7 \pm Sdc = \frac{ad-bc}{(b+d)(c+d)} \pm \frac{(a+b)(a+c)}{n(b+d)(c+d)}$$

where C_7 = Cole's Index of Interspecific Association

Sdc = standard deviation of Cole's index

n = total number of samples

and a, b, c, and d represented the four cells of the 2 × 2 contingency table.

Tests of statistical significance were performed by means of the Chi-square test. The Chi-squares were computed by the formula:

$$X^2 = \frac{(ad-bc)^2 n}{(a+b)(a+c)(c+d)(b+d)}$$

where X^2 = Chi-square value
n = number of samples

and a, b, c, and d represented the different cells of the 2 × 2 contingency table.

In all cases, a single degree of freedom was used. Chi-quare values greater than 3.84 were significant at the 5 percent level, while values greater than 6.63 were significant at the 1 percent level.

Data representation.— The three-dimensional graphic representation of data obtained from ordination analysis was drawn by the computer. Such representation was accomplished through the use of a plotting technique developed and programmed by Mr. Howard Jesperson, Agricultural Experiment Station, Iowa State University.

Results and Discussion

Marean and Jones (1903) gave the following description of the landscape in central Iowa:

> Low knolls are separated by saucerlike depressions in which impounded water often stands the year around. In many cases these low-lying areas have been reclaimed by artificial drainage, but in the main rainwater which falls upon the upland has to escape by seepage or evaporation. Little ponds and marshes are found in almost innumerable places scattered all over the country.

These saucerlike depressions have been estimated as covering more than 50 percent of that part of Iowa subjected to late Wisconsinan glaciation (Hewes 1950). They were early recognized as supporting a distinct vegetation from that of the adjacent upland prairie (Yapp 1909, Sherff 1912, Shimek 1915, and Berry 1927). The grasses of these areas were described as being "ten to twelve feet tall all season" (Dondore 1926). These and later descriptions indicate that the potholes and drainage ways were often characterized by very discrete zones of vegetation (Sherff 1912, Shimek 1915, Schaffner 1926,

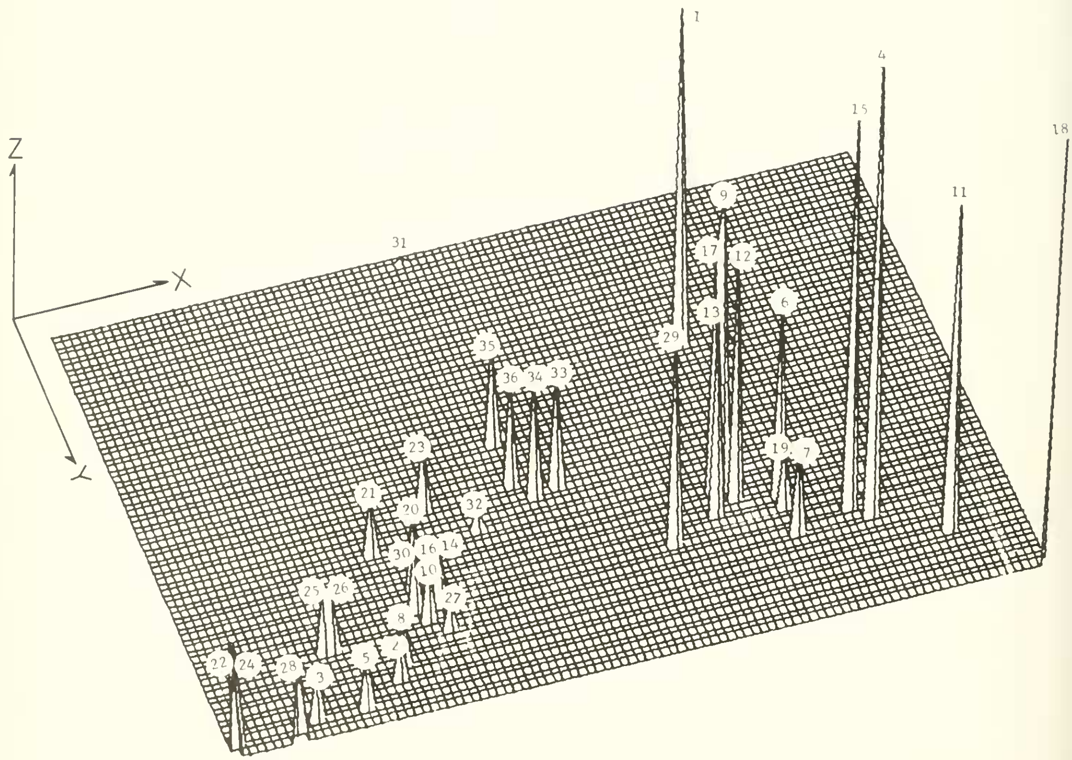

Fig. 2. Three-dimensional ordination of pothole and drainage zones found in Kalsow Prairie, with numbers corresponding to pothole and drainage numbers from Figure 1 except 33–36, which are prairie edge areas.

Hayden 1943, Trauger 1967). Three to four zones were generally recognized, yet in all cases little information was given on the relationships of these zones to one another either floristically or spatially. Some authors (Sherff 1912, Schaffner 1926, Hayden 1943), however, indicated that succession was taking place in these areas and proposed the following successional scheme:

I Pond center
II Sedge zone
III Slough grass zone
IV Dry margin of slough grass
V *Andropogon gerardi*
VI Upland prairie

Within the boundaries of Kalsow Prairie there exists a complex of 14 potholes and corresponding drainage ways (Fig. 1). These areas are found scattered throughout the 160 acres at different elevations. They also vary in depth and degree of fill. These characteristics make them extremely useful in studies of plant succession and zonation. All 14 potholes studied exhibited strong zonation. Each zone was subsampled 20 times for cover and then averaged to obtain a characteristic vegetation for each zone. The 36 zones were ordinated into three-dimensional space using Orloci's (1966) method (Figs. 2 and 3) and then clustered according to Sneath and Sokal (1973) (Fig. 4).

Following the ordination and cluster analyses, the zones were then grouped into six units as shown in Figures 3 and 4. This procedure seemed justified since each zone represented a rather discrete vegetational unit. After grouping, the data from all zones included in each new unit were averaged and placed in Table 1. These six groups (with one exception, Group 5) correpond in reality to the suggested successional sequence shown in Figure 5. Table 1 is so designed that columns 1 through 6 represent values from the center of each pothole through a transition to upland prairie, respectively. The positioning of each species within Table 1 was done by

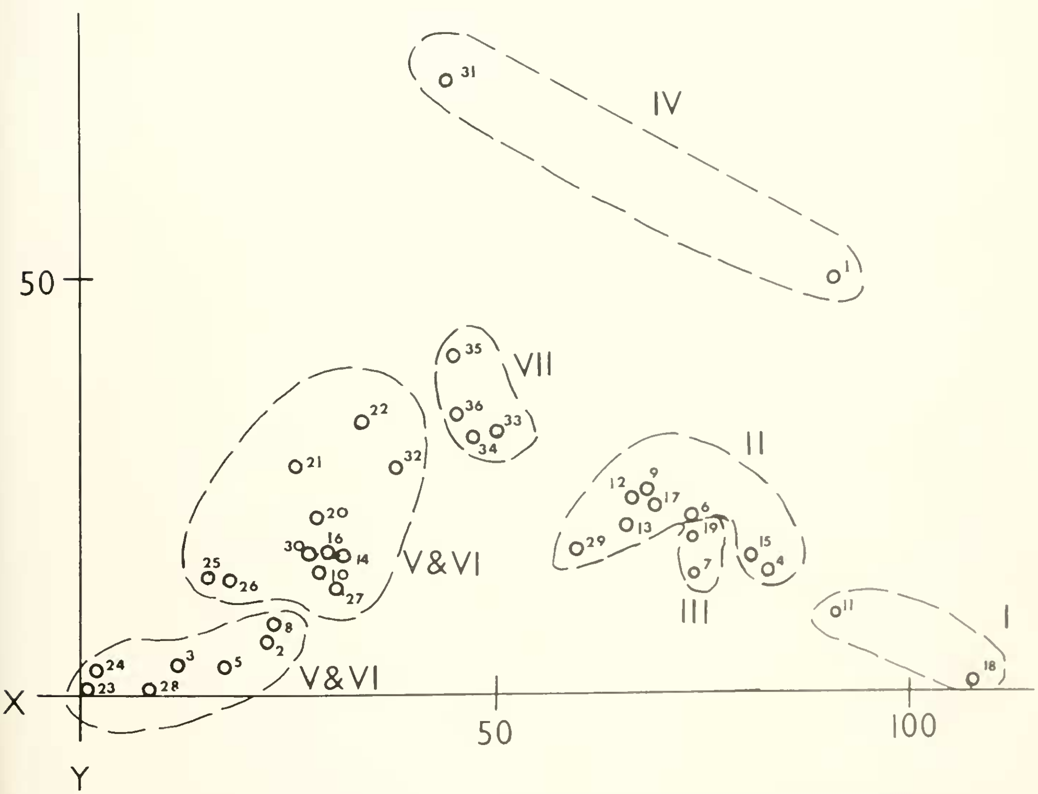

Fig. 3. Two-dimensional ordination of pothole and drainage zones of Kalsow Prairie, grouped as shown in Table 1 with minor exceptions. The factors responsible for the ordination are unknown.

TABLE 1. Average percentage cover values in the six groups according to Orloci ordination for the pothole and drainage communities.

Species	1	2	3	4	5	6
Polygonum coccineum[a]	66.15	26.74	31.15	5.27	2.58	.57
Lysimachia hybrida[a]	19.50	.39	–	.55	.36	.07
Scirpus fluviatilis[a]	5.55	22.94	1.55	.11	–	–
Carex atherodes[a]	2.45	10.56	53.45	.06	.12	–
Spartina pectinata[a]	–	1.89	.80	17.54	12.53	2.20
Carex aquatilis[a]	–	1.44	.75	14.51	3.42	6.05
Carex retrorsa	–	.80	.20	3.27	2.10	.02
Phalaris arundinacea	.05	.39	–	2.64	2.21	–
Sagittaria latifolia	–	–	–	1.21	.01	–
Eleocharis sp.	–	.20	.05	.73	.29	–
Calamagrostis canadensis[a]	–	2.60	3.15	26.73	57.10	6.42
Apocynum sibiricum	–	.40	–	.98	2.08	.75
Lycopus americanus	–	.24	–	.18	1.36	1.07
Convolvulus sepium	–	–	–	.16	.14	.12
Teucrium canadense	–	.41	–	.10	.76	.60
Carex meadii	–	–	–	.01	.26	–
Iris virginica	–	–	–	.01	.14	–
Asclepias incarnata	–	–	–	.07	.01	–
Hordeum jubatum	–	–	–	.01	–	–
Rumex crispus	–	–	–	.01	–	–
Panicum capillare	–	–	–	–	–	.02
Cirsium altissimum	–	–	–	–	–	.02
Asclepias sullivantii	–	–	–	–	–	.05
Zizia aurea	–	–	–	.01	–	.07
Pycnanthemum virginanum	–	–	–	–	–	.10
Elymus canadensis	–	–	–	.01	–	.15
Thalictrum dasycarpum	–	–	–	–	–	.15
Helenium autumnale	–	–	–	.01	–	.20
Helianthus laetiflorus	–	–	–	–	–	.20
Anemone cylindrica	–	–	–	–	–	.20
Solidago rigida	–	–	–	–	–	.20
Gentiana andrewsii	–	–	–	.01	.02	.20
Agrostis hiemalis	–	–	–	–	–	.22
Heliopsis helianthoides	–	–	–	–	–	.22
Cicuta maculata	–	–	–	–	–	.22
Lythrum alatum	–	–	–	.01	.21	.22
Aster ericoides	–	–	–	–	–	.25
Panicum virgatum	–	–	–	–	.07	.25
Lathyrum palustris	–	–	–	.02	.06	.35
Silphium laciniatum	–	–	–	–	–	.37
Eryngium yuccifolium	–	–	–	–	–	.40
Desmodium canadense	–	–	–	–	–	.40
Liatris pycnostachya	–	–	–	–	–	.55
Vernonia fasciculata	–	–	–	.24	.53	.55
Rosa suffulta	–	–	–	.32	.10	.72
Fragaria virginiana	–	–	–	–	.01	1.32
Senecio pauperculus	–	–	–	–	–	1.52
Solidago gymnospermoides	–	–	–	–	.17	1.70
Andropogon gerardi	–	–	–	–	–	2.20
Poa pratensis	–	–	–	.58	.60	2.35
Solidago canadensis	–	–	–	.01	.01	3.05
Sporobolus heterolepis	–	–	–	–	–	4.07
Aster simplex	.40	–	–	.86	2.01	5.22
Galium obtusum	–	–	–	.35	1.56	5.65
Carex lasiocarpa[a]	–	.55	1.15	5.55	7.43	10.15
Helianthus grosseserratus	–	–	–	.65	1.98	13.10

[a]Species picked by the three-dimensional ordination as indicator species.

assigning those species with the highest values for Group 1 at the top and those species with the highest values for Group 6 at the bottom of the list. It was then possible to determine from the table the characteristic distributional patterns of many of the species as well as their positions of importance within each zone (i.e., *Helianthus grosseserratus* is mainly restricted to Groups 5 and 6 and is the dominant species of Group 6).

The species of these different zones were also ordinated into three-dimensional space (Fig. 6). The ordination did not yield groups of strongly associated taxa but rather picked out eight species exhibiting distinct and different distributional patterns. It placed all other species within the areas covered by the circles A, B, and C. When the results of Figure 6 are compared with those of Table 1, it can be seen that the species picked by this method as indicator species are those taxa which represent the dominants or subdominants of Groups 1 through 6.

A 1000-foot bisect of the area noted in Figure 1 was taken in an effort to correlate the distribution of the dominants of each zone with elevation and topography. This information has been summarized in Figure 7. The data show that elevation changes of 6 to 12 inches altered the distribution patterns of the zone dominants.

Attempts to pick groups of associated species through the application of Cole's Index are shown in Table 2 and in Figures 8 and 9. Figure 8 represents a clearly definable cluster and includes the dominant species of Groups 1 through 3 of Table 1. These species are *Carex atherodes*, *Lysimachia hybrida*, *Poly-*

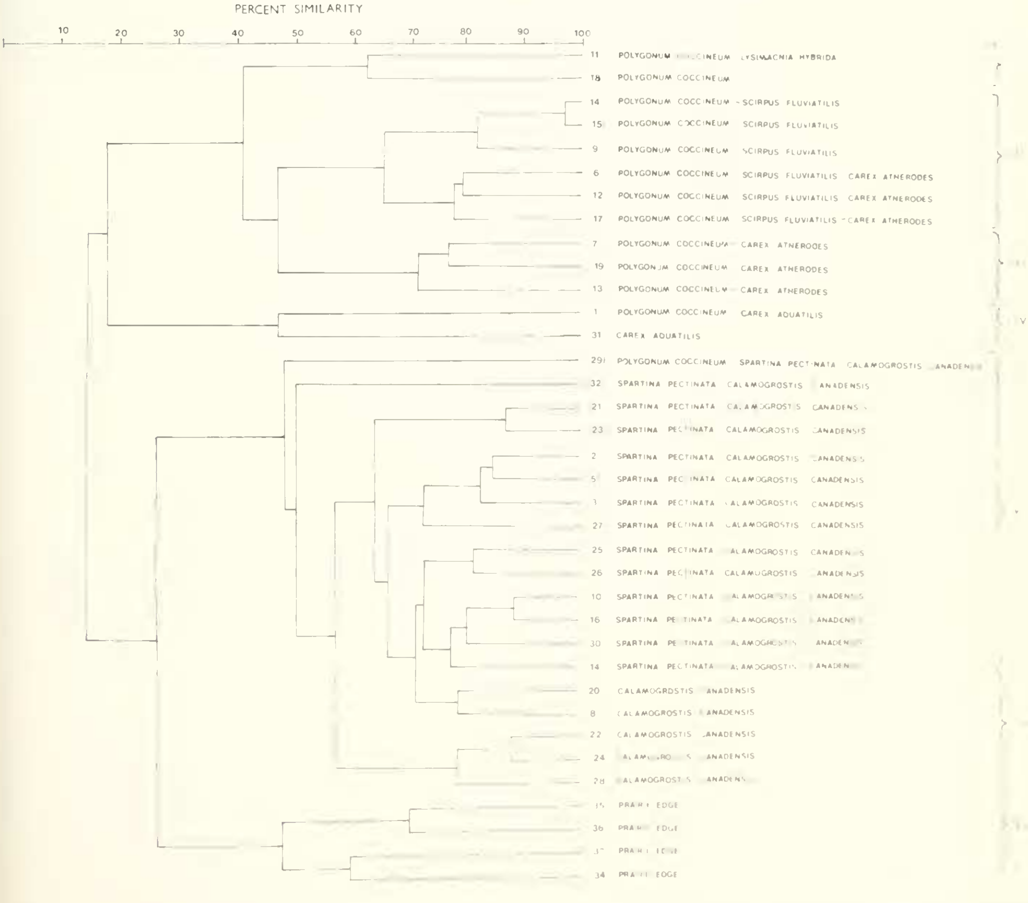

Fig. 4. Phenogram of 36 pothole zones as developed from cluster analysis (Sneath and Sokal 1973). Groups are as shown in Table 1 with minor exceptions.

gonum coccineum, and *Scirpus fluviatilis.* Figures 8b and 9 show several definable clusters and include taxa found in Groups 4 through 6 of Table 1. The cluster of species designated by A in Figure 9 contains species found entirely in Groups 4 and 5 of Table 1. Those clusters identified by the letters B and C of this same figure contain only plants found in Group 6 of Table 1 and correspond in reality to the prairie edge. Cluster A and Clusters B and C are bridged by a single species (*Aster simplex*) that is found growing mainly along the border between Groups 5 and 6 of Table 1.

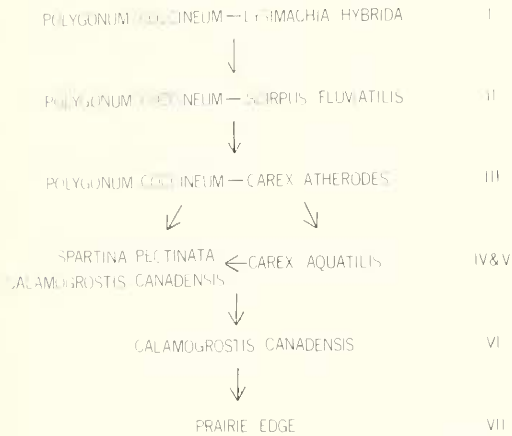

Fig. 5. Suggested successional sequence for potholes of Kalsow Prairie.

The vegetation of the potholes and drainage ways of Kalsow Prairie can best be described as a series of five zones (Fig. 5), each of which exhibits different spatial and floristic properties. This characteristic zonation can be expected to repeat itself from pothole to pothole when controlling environmental factors are similar. The zones themselves are best described by starting at the center of the potholes and moving toward the prairie edge. Zone 1 (Group 1 of Table 1, etc.) is found at the center of the deepest potholes and is

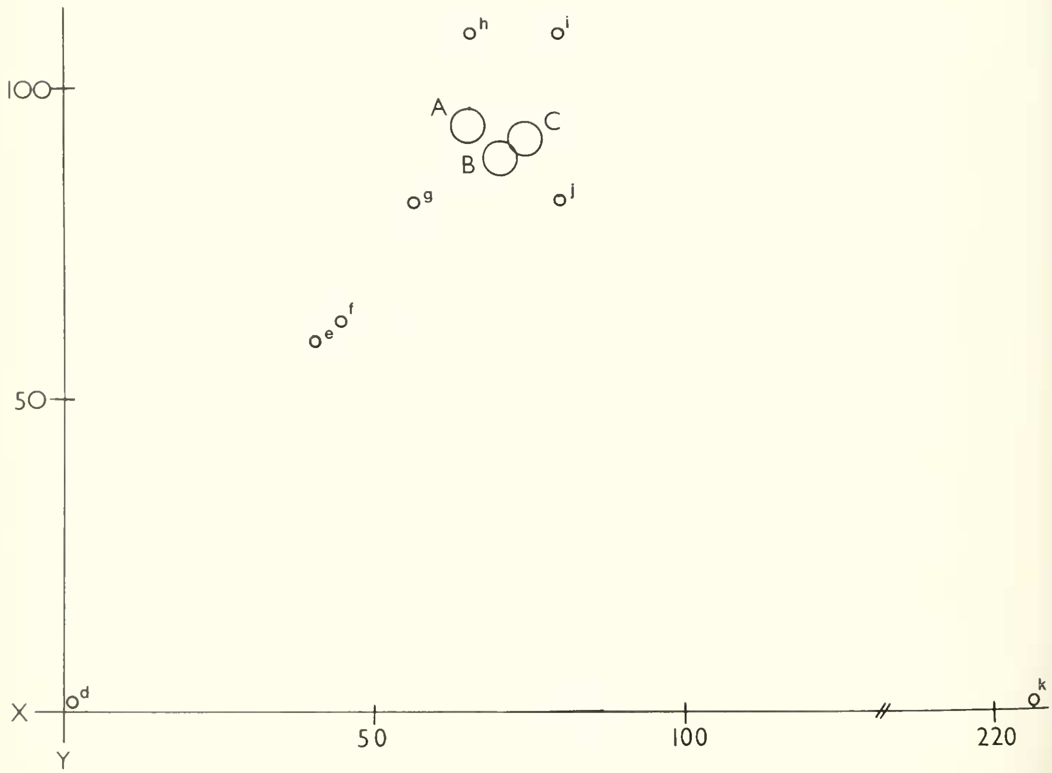

Fig. 6. Two-dimensional ordination of species found in pothole and drainage areas of Kalsow Prairie; A, B, and C = clusters of species not showing distinct distribution patterns, d = *Polygonum coccineum* (usually in center of pothole), e = *Scirpus fluviatilis*, f = *Carex atherodes*, g = *Lysimachia hybrida*, h = *Spartina pectinata*, i = *Carex aquatilis*, j = *Carex lasiocarpa*, k = *Calamagrostis canadensis* (usually in outer zone of pothole complex).

TABLE 2. Cole's Index values expressing positive interspecific association in pothole and drainage communities.

Species	Species	X^{2a}	$C_7{}^b$	Sd_{C_7}
Andropogon gerardi	Eryngium yuccifolium	119.80	.30	.02
	Liatris pycnostachya	130.35	.38	.03
	Sporobolus heterolepis	65.90	.22	.02
Anemone cylindrica	Fragaria virginiana	89.71	.19	.02
	Panicum virgatum	84.61	.24	.02
	Thalictrum dasycarpum	91.73	.33	.03
Apocynum sibiricum	Calamagrostis canadensis	41.22	.68	.10
	Carex lasiocarpa	30.42	.57	.10
	Carex retrorsa	9.44	.18	.05
	Spartina pectinata	19.63	.37	.08
Aster simplex	Calamagrostis canadensis	36.47	.56	.09
	Carex lasiocarpa	31.79	.51	.09
	Galium obtusum	212.39	.51	.03
	Helianthus grosseserratus	231.49	.51	.03
	Poa pratensis	85.80	.18	.01
	Spartina pectinata	19.10	.31	.07
Calamagrostis canadensis	Carex aquatilis	49.30	.17	.02
	Carex lasiocarpa	338.21	.68	.03
	Carex retrorsa	81.33	.19	.02
	Spartina pectinata	200.44	.41	.02
Carex atherodes	Polygonum coccineum	153.47	.93	.07
	Scirpus fluviatilis	120.34	.47	.04
Carex meadii	Rosa suffulta	28.47	.38	.07
Carex aquatilis	Carex lasiocarpa	73.33	.49	.05
	Carex retrorsa	53.85	.24	.03
	Spartina pectinata	19.61	.20	.04
Carex lasiocarpa	Carex retrorsa	111.72	.70	.06
	Spartina pectinata	183.90	.40	.02
Carex retrorsa	Spartina pectinata	43.76	.35	.05
Convolvulus sepium	Galium obtusum	8.76	.39	.13
Desmodium canadense	Aster ericoides	54.86	.28	.03
	Liatris pycnostachya	87.08	.42	.04
	Ratibida columnifera	200.56	.28	.02
	Senecio pauperculus	189.69	.71	.05
Eleocharis sp.	Phalaris arundinacea	28.62	.25	.04
Elymus canadensis	Aster ericoides	65.57	.33	.04
	Galium obtusum	4.34	.39	.18
	Helianthus grosseserratus	30.83	1.00	.18
	Lathyrus palustris	62.34	.49	.06
	Desmodium canadense	64.57	.33	.04
	Liatris pycnostachya	44.21	.32	.04
	Senecio pauperculus	33.25	.32	.05
	Thalictrum dasycarpum	91.73	.33	.03
Eryngium yuccifolium	Sporobolus heterolepis	54.86	.28	.03
Fragaria virginiana	Andropogon gerardi	37.61	.19	.03
	Galium obtusum	46.46	.70	.10
	Helianthus grosseserratus	104.86	1.00	.09
	Poa pratensis	19.29	.25	.05
	Senecio pauperculus	37.61	.19	.03
	Solidago canadensis	30.90	.27	.04
	Sporobolus heterolepis	75.87	.19	.02
Galium obtusum	Helianthus grosseserratus	242.41	.60	.03
	Poa pratensis	86.58	.20	.02
	Spartina pectinata	13.73	.29	.07
Helenium autumnale	Helianthus grosseserratus	5.54	.60	.25
Helianthus grosseserratus	Poa pratensis	131.97	.25	.02
	Solidago canadensis	112.89	.20	.01
Iris virginica	Poa pratensis	7.38	.29	.10
	Rosa suffulta	23.11	.32	.06
	Vernonia fasiculata	8.39	.29	.10

Table 2 continued.

Species	Species	X^{2a}	C_7^b	$Sd_{C_7}^c$
Lathyrus palustris	Poa pratensis	9.53	.20	.06
	Solidago gymnospermoides	62.18	.30	.03
	Thalictrum dasycarpum	75.89	.18	.02
Liatris pycnostachya	Senecio pauperculus	44.56	.29	.04
	Sporobolus heterolepis	248.50	.50	.03
Lysimachia hybrida	Polygonum coccineum	16.21	.61	.15
	Scirpus fluviatilis	16.11	.34	.08
Lythrum alatum	Vernonia fasciculata	5.46	.20	.08
Panicum virgatum	Poa pratensis	14.89	.29	.07
	Teucrium canadense	45.63	.39	.05
Poa pratensis	Solidago canadensis	92.29	.30	.03
Polygonum coccineum	Scirpus fluviatilis	223.30	.32	.02
Rosa suffulta	Andropogon gerardi	42.51	.21	.03
	Solidago canadensis	35.46	.30	.05
Solidago canadensis	Senecio pauperculus	160.63	.30	.02
Zizia aurea	Desmodium canadense	132.56	.66	.05

[a]Chi-square
[b]Cole's Index
[c]Standard deviation Cole's Index

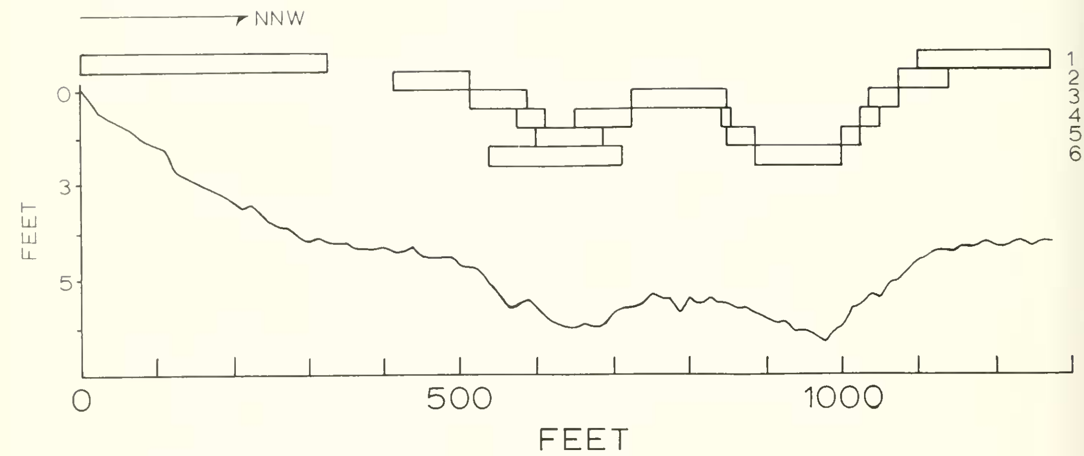

Fig. 7. Correlation of dominant species of each zone from potholes and drainages with changes in elevation along 1,000 ft (925 m) bisect; 1 = *Sporobolus heterolepis*, 2 = *Helianthus grosseserratus*, 3 = *Calamagrostis canadensis*, 4 = *Carex atherodes*, 5 = *Scirpus fluviatilis*, 6 = *Polygonum coccineum*.

dominated chiefly by *Polygonum coccineum* and *Lysimachia hybrida*. Zone 2 is found to completely encircle Zone 1 and is characterized by the dominants *Polygonum coccineum* and *Scirpus fluviatilis*. Zone 3 is found as a very narrow band that encircles Zone 2 or occurs as rather wide patches in areas of equivalent elevation. It is characterized chiefly by *Carex atherodes*. Zones 4 and 5 are best distinguished in potholes and drainage ways that are somewhat shallow. Zone 4 most often occupies the center of these shallow depressions surrounded by Zone 6. The dominant species (*Carex aquatilis*) of Zone 5 is usually found as a subdominant of Zone 4 but at times appears as a dominant zone surrounded by Zone 6. Whether this relationship is due to competition and/or environmental influences is unknown. Zone 4 is characterized by the species *Spartina pectinata*, *Carex aquatilis*, and *Calamogrostis canadensis*. Zone 6 is distinguished by the dominant species *Calamagrostis canadensis* and a few other participating species (i.e., *Apocynum sibiricum*, *Lycopus americanus*, *Teucrium canadense*, *Carex meadii*, and *Iris virginica*). Zone 7 and column 6 of Table 1 represent the prairie edge and are characterized primarily by the presence of *Helianthus grosseserratus*.

These zones appear to represent a successional sequence that is controlled basically by the degree of pothole fill and consequently by related moisture regimes. The successional scheme (Fig. 5) parallels in many respects a scheme proposed by earlier authors (Sherff 1912, Schaffner 1926, Hayden 1943).

The actuality of this scheme is based on the repeatability of the zonation pattern as found within the potholes of Kalsow Prairie. Evidence for change of fluctuations in pothole vegetation paralleling this sequence will depend on the results obtained from long-term studies.

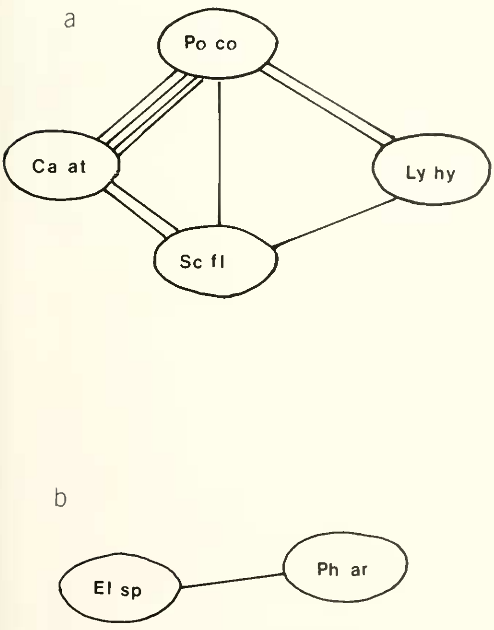

Fig. 8. Associated species of potholes and drainage, Groups 1 and 2 (Table 1) as determined by Cole's (1949) Index; (a) Ca at = *Carex atherodes*, Ly hy = *Lysimachia hybrida*, Po co = *Polygonum coccineum*, Sc fl = *Scirpus fluviatilis*; (b) El sp = *Eleocharis* sp., Ph ar = *Phalaris arundinacea*.

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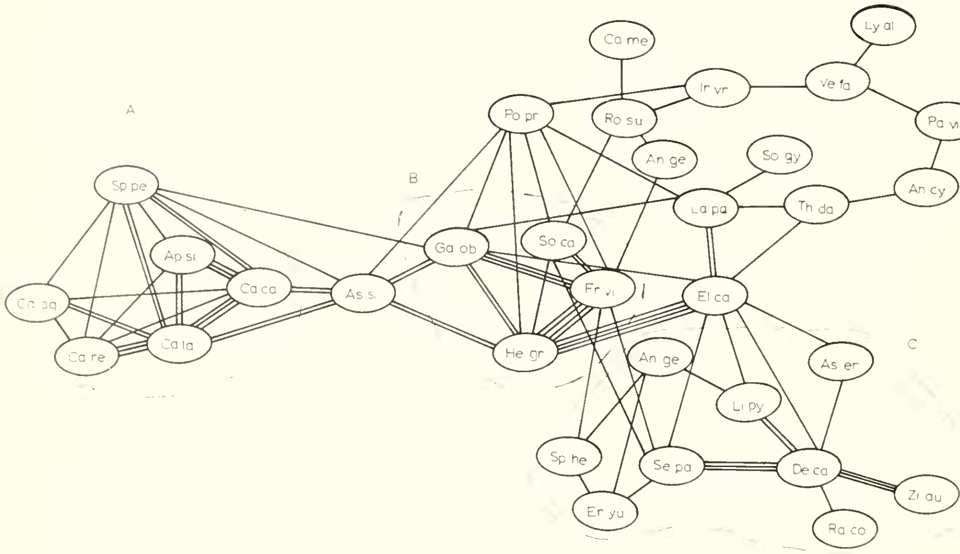

Fig. 9. Associated species of potholes and drainage, Groups 3–6 (Table 1) as determined by Cole's (1949) Index, the more lines between species, the greater the association; groups A, B, and C are basic clusters; An ge = *Andropogon gerardi*, An cy = *Anemone cylindrica*, Ap si = *Apocynum sibiricum*, As er = *Aster ericoides*, As si = *Aster simplex*, Ca aq = *Carex aquatilis*, Ca ca = *Calamagrostis canadensis*, Ca la = *Carex lasiocarpa*, Ca me = *Carex meadii*, Ca re = *Carex retrorsa*, De ca = *Desmodium canadensis*, El ca = *Elymus canadensis*, Er yu = *Eryngium yuccifolium*, Fr vi = *Fragaria virginiana*, Ga ob = *Galium obtusum*, He gr = *Helianthus grosseserratus*, Ir vr = *Iris virginica*, La pa = *Lathyrus palustris*, Li pu = *Liatris pycnostachya*, Ly al = *Lythrum alatum*, Pa vi = *Panicum virgatum*, Po pr = *Poa pratensis*, Ra co = *Ratibida columnifera*, Ro su = *Rosa suffulta*, Se pa = *Senecio pauperculus*, So ca = *Solidago canadensis*, So gy = *Solidago gymnospermoides*, Sp he = *Sporobolus heterolepis*, Sp pe = *Spartina pectinata*, Te ca = *Teucrium canadense*, Tha da = *Thalictrum dasycarpum*, Ve fa = *Vernonia fasiculata*, Zi au = *Zizia aurea*.

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